

The University of Chicago

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VARIATIONS IN ENVIRONMENT

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF BOTANY

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VEGETATIVE RESPONSES OF *BROMUS INERMIS* TO CERTAIN VARIATIONS IN ENVIRONMENT¹

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 587

JOHN C. DIBBERN

Introduction

Smooth brome grass (*Bromus inermis* Leyss.) has long been cultivated in Hungary and Russia. The first recorded importation of seed into the United States was in 1880, and many importations from different sources have been made since. From these importations our present strains have been developed.

The species is now found as far south as Tennessee, Kansas, and California and extends northward through Canada into Alaska. On mountain ranges in the semiarid regions of the West and Northwest it is frequently found at all elevations up to 9,000 feet, and in central Utah up to 10,500 feet, though it does not reseed at this elevation (3). It is important as a hay and pasture grass, especially from Minnesota and Kansas to eastern Oregon and Washington, occasionally

eastward to Michigan and Ohio; and in the artificial reseeding of denuded range land in regions of light rainfall and moderate summer temperatures.

Smooth brome is a perennial and spreads vegetatively by means of rhizomes. It grows rapidly in the spring and, though remaining green throughout the warm summer months, then makes very little additional growth. Inflorescences develop in the spring, and anthesis occurs in early summer. Through environmental selection northern and southern strains have evolved, these strains maturing late and early, respectively, when grown in the latitude of Lincoln, Nebraska (8). Within these strains the individual plants show a great diversity of growth habit, ranging from bunch types to semicreepers.

A study has been made of some of the vegetative responses of diverse plants of smooth brome grass to variations in clipping frequency, soil temperature,

¹ This work was aided in part by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

shading, and container size in an attempt to shed some light on (a) the ability of the species to withstand grazing or mowing; (b) its limitation in distribution to only the higher latitudes; (c) its shade tolerance; and (d) the type of container that will allow maximum growth in the greenhouse. The experiments were conducted in the greenhouses and garden of the University of Chicago from the spring of 1946 through early summer, 1947.

Material and methods

Because of the diversity of the species, it seemed desirable to work with a wide variety of plants. To this end the clonal and seed materials used represent plants originating from Saskatchewan to Washington, Kansas.

In greenhouse experiments the soil used consisted of three parts loam soil of prairie origin mixed with one part sand. A supplementary nitrate solution was occasionally applied and consisted of 3.5 gm. $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ per liter of water.

In experiments where both root and top weights are reported, the separation of tops and roots was made on a morphological basis rather than at the ground level. Underground stem parts were thus considered part of the tops. Where root weights were not taken, tops were clipped at a height of 2 inches above the ground level except where specifically stated otherwise.

Stem counts represent only those stems that had emerged from the soil, including both elongated and unelongated tillers, but do not include dead stems.

Experimentation

CLIPPING

GREENHOUSE SERIES.—On April 27 and 28, 1946, six divisions of each of twenty-three clones which had been

growing outdoors either at Chicago, Illinois, or at Madison, Wisconsin, were planted separately in 8-inch unglazed clay pots on well-illuminated benches in the greenhouse. Each division consisted of approximately six stems and accompanying roots. The leaves of plants that showed severe wilting after planting were clipped to decrease water loss, but in no instance was the clipping severe enough to remove entire leaf blades or growing points. Nitrate solution (192 ml.) was supplied to each plant on May 4, 1946, September 5, 1946, and April 3, 1947, and they were watered when necessary.

On June 30, 1946, the three most uniform divisions of each clone were selected for experimentation, but only the seventeen clones in which all three divisions survived until the termination of the experiment are reported upon. Series C was an unclipped control, series 1 was clipped on June 30, 1946, and series 2 on June 30 and September 27.

Because of general lack of vigor, a final harvest was considered inadvisable in the fall, and the effects of clipping for the 1946 season are therefore shown only by stem counts (table 1).

The clipping on June 30 caused a reduction in the number of stems in series 1 to 76% as measured on July 13, but series 2 was reduced to only 86%. The stem counts and top weights on June 30 were larger in series 2 than in series 1, and it would thus appear that the larger plants were less affected by clipping than were the smaller ones.

On September 27 the stem count of series 1 was 2% below the count on June 30, and that of series 2 was 23% above. The yield of tops in series 2, however, was less than half that of June 30. The lower yield between June 30 and September 27 cannot be considered entirely an effect of the first clipping. Growing con-

ditions in the greenhouse during this period were quite adverse. Daytime soil temperatures averaged 23°C ., and maximum air temperatures 33°C . The plants also became infested with mealy bugs, aphids, and red spiders, and, in addition to the injuries so caused, there was some injury from control spraying.

On November 24, stem counts showed the control to have increased 97% over the value on June 30, series 1 had in-

size, as suggested by the results with different-sized containers (see soil-volume experiment). On April 25 the three series were clipped back to 2 inches. The relative yields produced between April 25 and June 2, and the relative numbers of stems on June 2, 1947, when the experiment was terminated, are taken as a measure of the aftereffects of no clipping, one clipping, and two clippings the previous year. If the top growth produced

TABLE 1
STEM COUNTS AND DRY WEIGHTS OF TOPS IN GREENHOUSE CLIPPING EXPERIMENT

SERIES	1946				1947			1946		1947	
	6/30	7/13	9/27	11/24	1/18	3/31	6/2	6/30	9/27	4/25	6/2
	No. of stems*							Dry wt. of tops (gm.)*			
C.....	292	378	530	575	559	540	527			46.19	35.20
1.....	246	186	241	276	270	316	290	59.14		30.59	22.87
2.....	305	263	375	280	269	278	282	74.46	35.28	19.94	20.71
	No. of stems in % of count on 6/30							Dry wt. per stem (gm.)			
C.....	100	129	182	197	192	185	180			0.086	0.067
1.....	100	76	98	112	110	128	118	0.240		.097	.079
2.....	100	86	123	92	88	91	92	0.244	0.094	0.072	0.073

* Sums of values for seventeen clones.

creased 12%, and series 2 had decreased 8%. During the period from November 24, 1946, to January 18, 1947, the light intensity was quite low in the greenhouse, and all three series showed a decrease in the number of live stems.

By March 31, 1947, the plants had resumed active growth, and both clipped series showed an increase in stem numbers over the January count. However, the stem count of series C showed a decrease from the January count. This decrease might indicate that the volume of soil in the 8-inch clay pots had become a limiting factor to further increase in

between April 25 and June 2 is converted to dry-weight yield per stem based on the counts of June 30, 1946, the value for series 1 is 23% less, and that of series 2 is 43% less, than the control. The stem counts on June 2, 1947, show that series C had 80% more and series 2 had 8% less than on June 30, 1946.

HARRISON and CRAWFORD (5) found in a field experiment with smooth brome that applications of ammonium sulfate had more effect upon stem size than upon total number of stems in determining yield of forage. The total dry-weight yields in this clipping experiment, how-

ever, showed much closer correlation with stem counts than with average weight per stem (table 1).

GARDEN SERIES.—On April 25, 1946, six divisions of each of twenty-two clones were planted in six plots laid out side by side in an east-west direction in the garden. Each division consisted of approximately six stems and their roots and was taken from plants growing outdoors either at Chicago, Illinois, or at Madison, Wisconsin. The leaves of plants that showed severe wilting after planting were clipped to decrease water loss, but in no instance was this clipping severe enough to remove entire leaf blades or growing-points. The divisions were spaced 18 inches apart in the east-west direction and 24 inches apart in the north-south. The plants were watered sufficiently to prevent deficiency at any time. On June 24, 1946, the three most uniform divisions of each clone were selected for the clipping experiment.

Series C was an unclipped control, series 1 was clipped on June 24, and series 2 on June 24 and August 23. On November 15 all three series were clipped back to 2 inches and the total oven-dry yield of tops was determined. On June 7, 1947, the three series were clipped again to 2 inches, and the relative dry-weight yields were used as a measure of the aftereffects of clipping treatments in the preceding year.

The first stem count was made on June 24, 1946, at the time series 1 and series 2 were clipped the first time. The larger dry weight of tops which had been produced by series 2 was accounted for partially by the greater number of stems and partially by the greater weight per stem (table 2).

On August 23, when series 2 was clipped a second time, the numbers of stems in series 1 and series 2 were sub-

stantially greater than the numbers on June 24, though less than in the control. In contrast to the low yield from the second clipping of plants in the greenhouse, the second clipping in the garden yielded several times as much dry matter as the first, and the weight per stem was over 50% greater (table 2). This contrast is quite sharp and, even though there were five additional clones included in the garden experiment, emphasizes the differences between growing conditions outdoors and in the greenhouse.

On November 15 a stem count was made, and all three series were clipped to determine the total yields in 1946. The relative stem count was 27% less in series 1 and 55% less in series 2 than the control. The weight per harvested stem was 5% less in series 1 and 43% less in series 2 than the control. The total top weight per original stem (based on count of June 24) was 24% less in series 1 and 30% less in series 2 than the control.

From the clipping of June 7, 1947, the dry-weight yield per original stem (count of June 24, 1946) was 21% less in series 1 and 56% less in series 2 than the control.

Although these plants which grew outdoors made a much more vigorous growth than those in the greenhouse (tables 1 and 2), as measured by stem counts, top yields, and individual stem weights, the aftereffects of clipping the preceding season are very similar in greenhouse and garden as measured by the percentage differences between the 1947 yields per stem (count of June 24 and June 30, 1946) in series C, series 1, and series 2.

SEEDLINGS.—On April 30, 1947, five 8-inch glazed pots were planted with caryopses of a southern strain (no. 25); five with a strain of intermediate latitude (no. 27); and five with a northern strain (no. 26). The caryopses were covered

with $\frac{1}{4}$ inch of sifted soil, and the pots were placed on a well-illuminated bench in the greenhouse. The seedlings were watered whenever necessary to prevent water deficit and were thinned to ten per pot on May 27. On June 2, one pot (no. 1) of each strain was harvested, and oven-dry top and root weights were determined. On the same day the plants in pots 2, 3, and 4 of each strain were

This point is emphasized, since it is pertinent to the effects of clipping upon top and root development.

Pot no. 2 of each strain, harvested 6 days following clipping on June 2, showed a higher T/R ratio in the southern and northern strains, but a lower T/R ratio in the central strain, than pot no. 1, which was harvested without being clipped (table 3).

TABLE 2
STEM COUNTS AND DRY WEIGHTS OF TOPS IN GARDEN CLIPPING EXPERIMENT

SERIES	1946				1947	1946				1947
	6/24	7/13	8/23	11/15	5/12	6/24	8/23	11/15	Total	6/7
	No. of stems*					Dry wt. of tops (gm.)*				
C.....	357	665	1896	8401	8127			1768.66	1768.66	3607.5
1.....	302	344	1169	5213	5252	72.43		1062.03	1134.46	2412.5
2.....	434	505	1769	4675	4784	129.17	828.79	550.36	1508.32	1965.0
	No. of stems in % of count on 6/24					Dry wt. per stem (gm.)				
C.....	100	186	531	2375	2276			0.21		
1.....	100	114	386	1726	1739	0.24		.20		
2.....	100	116	408	1077	1102	0.30	0.47	0.12		

* Sums of values for twenty-two clones.

clipped back to 4 inches high. On June 8, pot no. 2 was harvested and pot no. 3 was again clipped back to 4 inches. On June 14 the remaining pots (nos. 3, 4, and 5) were harvested, and oven-dry top and root weights were obtained (table 3).

In all three strains the top-weight/root-weight ratio (T/R) of unclipped seedlings harvested on June 2 was greater than for unclipped seedlings harvested 12 days later (pots 1 and 5). The increase in root weight in proportion to top weight as the seedling matures results from the increasing synthesis of carbohydrate by the photosynthetic tissue, which appears to have first priority on the seed reserves.

Plants clipped twice (pot 3) and once (pot 4) before harvesting produced less total top weight than the control (pot 5). The effect of clipping the tops in limiting the growth of roots was even greater than it was upon the tops and is reflected in the T/R ratios. In strains 25 and 27 the root weight in pot 3 harvested on June 14 is approximately the same as in pot 1 harvested on June 2—no net increase in root weight in 12 days when the tops were clipped twice.

DISCUSSION.—The results of both the greenhouse and the garden clipping experiments show conclusively that both the top yield per original stem and the num-

ber of stems were inversely proportional to the frequency of clipping and that these effects were carried over into the following growing season. With *Bromus inermis* HARRISON and HODGSON (6) also found that frequent and close clipping reduced both the amount of root growth and the total yield of tops and that, when the plants were completely defoli-

carbohydrate reserves was influenced less by the frequency than by time and degree of clipping. The period of reproduction from flower-stalk elongation to formation of ripe seed is critical, and clipping at this time seems to limit subsequent storage.

The direct cause of the limitation of top growth resulting from clipping is re-

TABLE 3
DRY WEIGHTS OF TOPS AND ROOTS AND T/R RATIOS FOR SEEDLING
CLIPPING EXPERIMENT*

STRAIN	POT NO.	TOP WT. (GM.)				ROOT WT. (GM.)	T/R
		6/2	6/8	6/14	Total	6/14	
25.....	1	0.55			0.55†	0.12†	4.6†
	2	0.35‡	0.47		0.82§	0.14§	5.9§
	3	0.30‡	0.13‡	0.37	0.80	0.12	6.7
	4	0.30‡		0.83	1.13	0.22	5.1
	5			1.89	1.89	0.61	3.1
27.....	1	0.64			0.64†	0.12†	5.3†
	2	0.36‡	0.53		0.89§	0.18§	4.9§
	3	0.35‡	0.18‡	0.41	0.94	0.13	7.2
	4	0.38‡		0.84	1.22	0.26	4.7
	5			2.17	2.17	0.62	3.5
26.....	1	0.30			0.30†	0.07†	4.3†
	2	0.22‡	0.48		0.70§	0.13§	5.4§
	3	0.20‡	0.16‡	0.49	0.85	0.20	4.2
	4	0.21‡		0.67	0.88	0.22	4.0
	5			1.46	1.46	0.52	2.8

* Values are sums of ten plants in each pot.

† On June 2.

‡ Clipped to 4 inches.

§ On June 8.

ated, new top growth was developed in a large measure at the expense of previously deposited root reserves. McCARTY and PRICE (7) found that the quantity of reserve carbohydrate stored in roots and stem bases of mountain brome and slender wheatgrass growing on the Wasatch Plateau of Utah was related to the amount of foliage present during the normal storage period of August and September and was less when the interval between earlier clipping and the normal storage period was shortened. Their results also indicated that the amount of

lated primarily to the reduction in photosynthetic tissue and to the use of reserves in the growth of new tops but is probably also markedly influenced by the concomitant limitation on root growth. The seedling experiment in the greenhouse showed that root growth was even more severely affected by clipping than was top growth. ROBERTSON (9) also found with *B. inermis* that, as a result of repeated clipping of tops, the rate of root growth diminished gradually until it ceased entirely, followed by a dying back from the root tips.

The findings of numerous workers (1, 2, 12) indicate that the greater yield of unclipped grass over periodically clipped grass is largely of fiber and other nitrogen-free substances. However this may affect the feeding value of the forage, one must not lose sight of the fact that the effects of clipping upon root growth and upon storage of reserves do govern over a period of years a perennial plant's ability to withstand adverse environmental conditions. This is brought out in the contrast between the stem counts in the garden experiment (table 2) and the greenhouse experiment (table 1). The general lack of vigor of the plants in the greenhouse clipping experiment which were also subjected to high temperatures and low light intensity lends stress to the point made by GRABER (4) that the productive capacity of grasses depends upon adequate supplies of available nutrients and moisture combined with favorable light and temperature conditions as well as upon adequate food reserves.

SOIL TEMPERATURE AND CLIPPING

In an attempt to determine the effects of soil temperature combined with clipping upon different types of brome grass, clone 4, a creeper from Washington; clone 11, a Parkland bunch type; clone 25, a southern type, with origin at Superior, Nebraska; and clone 26, a northern type with origin at Mandan, North Dakota, were selected for experimentation. The divisions of clones 4 and 11 were made by slicing uniform-sized root segments and accompanying stems from uprooted plants that had been established in the garden; those of clones 25 and 26 by slicing into uniform segments plants that had been established in 6-inch pots in the greenhouse. The root mass of the divisions of each clone was relatively uniform, but the accompany-

ing stem numbers varied greatly. The divisions were planted in 8-inch glazed pots on August 24, 1946, without any removal of leaf tissue, and were watered when necessary. By September 17 the plants appeared well established and were subjected to soil temperatures of 20°, 26°, and 31° C. by means of the University of Chicago soil temperature tanks. Because of limited facilities only one division of each clone in the unclipped series was subjected to each temperature. For the clipped series, clones 25 and 26 were run singly and clones 4 and 11 in duplicate; they were clipped on October 2. All plants were harvested on November 12, and the dry weights of both roots and tops and the numbers of roots were determined.

Only clones 25 and 4 survived clipping at all soil temperatures. Clone 11 survived clipping at 20° and 26° C., clone 26 only at 20°. The survival of clone 25 and death of clones 26 and 11 at the higher temperatures was possibly related to latitude of origin. This would agree with the observations of NEWELL and KEIM (8) that southern strains were more tolerant of midsummer heat and drought than northern strains. It was quite evident that removal of photosynthetic tissue accompanied by the rapid respiratory rate induced by high root temperatures was very unfavorable for even the strains that survived.

The root systems developed at the lowest temperature were fibrous and much branched, while at the highest temperature few roots of the second and third order were in evidence. STUCKEY (10), working with colonial bent grass, also found maturation of roots to be accelerated by higher soil temperatures, with little branching in evidence.

Total root weight was inversely correlated with soil temperature in all four

clones (table 4), as was the weight of individual roots. The data reflect markedly the limiting effects of high soil temperature upon root growth in this species and also the limiting effect of clipping.

The total numbers of roots of the three clones of northern origin in the unclipped series were also inversely related to soil temperature. However, clone 25, of southern origin, showed the maximum root number at 26° in the unclipped series. In the clipped series the inverse relation to temperature held for all clones except no. 4, where the lowest number of roots was found at 26° C. With the exception of clone 4 at 20° C. and clone 25 at 31°, the numbers of roots were lower on all the clipped plants than on the unclipped plants, irrespective of soil temperature.

Although in general the numbers and dry weights of stems were inversely correlated with soil temperature (table 4), the effects were not so marked as in the roots. Since the underground parts of the stems were subjected directly to the different temperatures, the results do not differentiate the direct from the indirect effects of soil temperature upon the stems.

With the exception of clone 4 at 20° the number of stems of all clones decreased as an effect of clipping, with greater decrease at higher soil temperatures. In the unclipped series one northern clone (no. 11) decreased in live stem number at the highest soil temperature; and the percentage increase in the others was least at the highest temperature. In the southern clone (no. 25) the greatest increase was at 26°.

Total top weight in the unclipped series was inversely correlated with soil temperature in two of the northern clones (26 and 11). Clone 4 yielded most at 20° C., with a slightly greater yield at

31° than at 26°. The southern clone (no. 25) produced the greatest top weight at 26° and the least at 31° C.

In the clipped series the data do not include the weights of tops clipped on October 2. In all clipped plants the final yields at 20° C. exceeded those at 26° or 31°, although in clone 26 the yield at 26° was near that at 20°.

The weight per stem in the unclipped series was inversely correlated with soil temperature for clones 26 and 11 but directly so for clone 4. Clone 25 had the greatest weight per stem at 26° C. and the least at 20°. The surviving plants in the clipped series had the lightest stems at 20° C. with the exception of clone 4 (table 4). This tendency toward fewer but heavier stems in the clipped plants at higher soil temperatures could result from an inhibition in either the initiation or elongation of new tillers with the consequent utilization of available nutrients and reserves by the surviving stems.

A measure of the total yield in proportion to the initial size of the clonal divisions was derived by dividing the final dry top weight by the stem numbers on September 17. In the unclipped series this value in two of the northern clones was inversely correlated with temperature, while in clones 25 and 4 it was greatest at 26° C. Clone 4 showed the least yield at 31° C.

In the clipped series all clones produced less dry-weight yield of tops per root at the higher temperatures, except clone 25, in which it was highest at 26° C. In the unclipped series this value was inversely correlated with soil temperature except in clone 4, in which it was highest at 20° C. and lowest at 26°.

The top-weight/root-weight ratio and weight-per-stem/weight-per-root ratio were positively correlated with soil temperature. This trend in these ratios is

TABLE 4
EFFECTS OF SOIL TEMPERATURE AND CLIPPING

SOIL TEMPERA- TURE (° C)	CLONE							
	25		26		4		11	
	Unclipped	Clipped	Unclipped	Clipped	Unclipped	Clipped	Unclipped	Clipped
Dry wt. of roots (gm.)								
20.....	0.83	0.58	1.30	0.21	5.20	2.01	4.25	0.74
26.....	.79	.33	0.53	0.20	1.94	0.36	1.41	0.57
31.....	0.11	0.05	0.17	0.08	0.99	0.42	0.43	0.10
Wt. per root (mg.)								
20.....	9	8	5	2	27	9	19	5
26.....	7	7	2	2	10	4	11	4
31.....	3	1	1	1	6	4	4	1
No. of roots								
20.....	90	77	265	114	195	220	219	145
26.....	113	50	257	114	189	99	134	129
31.....	37	43	150	88	163	118	121	88
Dry wt. of tops (gm.)								
20.....	2.19*	0.85†	3.81*	0.89†	13.73*	4.78†	15.47*	1.90†
26.....	2.46*	.71†	1.74*	0.89	9.68*	1.26†	7.80*	1.20†
31.....	0.64*	0.36†	0.71*	0.36	9.80*	1.41†	3.12*	0.36
Wt. per stem (mg.)								
20.....	104*	57†	93*	81†	270*	150†	430*	130†
26.....	135*	71†	76*	81	320*	130†	340*	150†
31.....	128*	72†	65*	65	360*	180†	170*	150
Relative no. of stems†								
20.....	150	83	186	79	196	100	133	68
26.....	200	71	121	79	187	50	135	33
31.....	125	45	110	110	104	40	90	110
Dry wt. of tops per root (mg.)								
20.....	24*	11†	14*	8†	70*	22†	71*	13†
26.....	22*	14†	7*	8	51*	13†	58*	9†
31.....	17*	8†	5*	5	60*	12†	26*	9

* Based on total top yield.

† Based on top yield produced after clipping on October 2.

‡ Number of stems on November 12 as percentage of number on September 17.

§ Dead.

TABLE 4—*Continued*

SOIL TEMPERA- TURE (° C)	CLONE							
	25		26		4		11	
	Unclipped	Clipped	Unclipped	Clipped	Unclipped	Clipped	Unclipped	Clipped
	Total top wt./total root wt.							
20.....	2.6*	3.3*	2.9*	7.1*	2.6*	5.9*	3.6*	10.8*
26.....	3.1*	7.0*	3.3*	§	5.0*	13.0*	5.5*	15.2*
31.....	5.8*	13.2*	4.2*	§	9.9*	25.3*	7.2*	§
	Wt. per stem/wt. per root							
20.....	11		19		10		22	
26.....	19		36		32		32	
31.....	43		59		60		47	

related primarily to the strong inverse correlation of root weights, both total and individual, with soil temperature. The adverse effect of clipping upon root growth is indicated by a comparison of the top-weight/root-weight ratios in the clipped series with the unclipped series (table 4).

In this experiment soil temperature exerted relatively greater control over root development than it did upon growth of the tops. Under the conditions of this experiment, adequate moisture was supplied to all plants, and the tops probably did not suffer water deficiency because of inadequate root systems, even at the highest soil temperature. Under field conditions, however, such limitation on root growth with the advent of warm soil temperatures accompanied by lack of moisture in the upper layers of soil would not be conducive to the survival of this species in competition with better adapted species, especially if grazed or mowed simultaneously. The lack of vigor observed in the plants clipped during the summer of 1946

in the greenhouse clipping experiment (table 1) was no doubt in part caused by the removal of photosynthetic tissue with consequent reduction in the synthesis of carbohydrate at the same time that the roots were subjected to high daytime soil temperatures bringing about an increased rate of respiration.

SHADING

Three divisions of the same twenty-three clones used in the greenhouse clipping experiment were used in an experiment on shade tolerance set up at the same time. The plants grew in the full natural light of the greenhouse until June 30, 1946, and were then apparently well established. They were then clipped back to a height of 2 inches but were not clipped thereafter. They were watered as necessary, and each plant was given 192 ml. of nitrate solution on May 4, 1946, on September 5, 1946, and on April 3, 1947. Series C remained in the full greenhouse light; series 1 was shaded by a single thickness of unbleached sheeting of a type used for shade-grown tobacco,

and series 2 by a double thickness. The average values of approximately simultaneous light readings made with a Weston Sunlight Meter during the course of this experiment were: outside, 5233 foot-candles; greenhouse, 2417 f.-c.; under one thickness of sheeting, 731 f.-c.; under two thicknesses of sheeting, 251 f.-c., or a ratio of approximately 100:46:14:5.

By September 27 only four clones had survived in series 2. At the termination of the experiment on June 2, 1947, all series 2 plants had died, but ten clones were still surviving in series 1. The clones which survived longest under the double thickness of cloth were among those surviving under the single thickness almost 8 months later. Six of the plants in series C had died by the termination of the experiment. Two of these were clones that survived in series 1, though not in series 2, and the other four died at about the same time as they did in series 1. Although the light intensity in the greenhouse was less than half that in full sunlight, some factor or factors other than low light intensity must have been the cause of death in most series C plants, as all but one died during the summer and fall of 1946. The same conditions of high air temperatures and infestation with greenhouse pests enumerated in the greenhouse clipping experiment prevailed during the course of this experiment and made growing conditions for all series decidedly adverse. The initial clipping and consequent limitation of photosynthetic tissue in all series, coupled with high air and soil temperatures and lowered light intensity, were quite favorable for a high rate of respiration and limited production of photosynthate.

WATKINS (11) found in a field experiment with *B. inermis* that a reduction of light intensity to 300-800 foot-candles

brought about a decrease in the number of shoots, number of rhizomes, number of fertile shoots, and dry weight of all plant parts, and an increase in the number of elongated internodes and in height of the plant. The effects of shading in the present experiment suggest inherent differences in the shade tolerance of the different clones. There seemed to be little correlation of shade tolerance with latitude of origin, since one of the surviving clones in series 2 had its origin in Washington, Kansas, and one in Saskatchewan. Neither did there seem to be any correlation with growth habit, as clones that were characteristically creepers as well as those that were bunch types were found among both the surviving and the dead plants in all series.

Under field conditions, where the plants grow close together and competition for light as well as for mineral nutrients and water is keen, those individuals that were not tolerant of shading would most certainly be crowded out. Ability to withstand shading, although of selection value in a field of pure brome grass, would be even more important in mixed fields of brome and alfalfa in which the presence of shade-tolerant strains might well determine the survival of brome grass in the mixture.

SOIL VOLUME

Equal divisions of four different clones which had been growing in the garden were planted in containers of seven different types and sizes on August 29, 1946, in an attempt to find what effect soil volume might have upon vegetative growth under greenhouse conditions. Tops and roots were trimmed as little as possible in transplanting, and all conditions under which the plants were grown were similar except the volume of soil in the different containers, the shape of the

containers, and the material of which the containers were constructed (table 5). Although each plant was given water as seemed to be necessary, rapid evaporation through the walls of the smaller unglazed clay pots probably removed the available water from the outer part of the soil mass so rapidly that the plants in these containers did not have sufficient moisture available to them at all times

over the surface of the soil, with some emerging from the space between the soil and the edge of the container. Root distribution was somewhat less uniform and was different for different clones, though in general the roots were well distributed throughout the soil in the larger containers and tended to be concentrated around the bottom and sides of the smaller ones. The roots of all clones in the

TABLE 5
RESULTS IN SOIL-VOLUME EXPERIMENT

Container	Relative soil volume	Original stem count	Final stem count	Final stem count as % of original	Total top wt. (gm.)	Top yield per original stem (gm.)	Av. wt. of each stem (gm.)	Total root no.	Total root wt. (gm.)	Av. wt. of each root (mg.)	T/R	Roots per stem	Top yield per root (mg.)	Wt. per stem/wt. per root
12-in. square wooden box.	12	22	150	682	35.13	1.6	0.23	754	5.42	7.2	6.5	5.0	4.7	32
12-in., deep clay pot*...	10	26	139	534	38.92	1.5	.28	795	8.98	11.3	4.3	5.7	4.9	25
8-inch, glazed crock†.....	4	28	133	475	38.56	1.4	.29	880	8.15	9.3	4.7	6.6	4.4	31
10-in., deep clay pot*...	5	26	114	439	28.93	1.1	.25	590	8.11	13.7	3.6	5.2	4.9	18
10-in., shallow clay pot*...	2	27	85	315	13.66	0.51	.16	457	3.74	8.2	3.7	5.4	3.0	20
8-in., deep clay pot*.....	2	26	79	304	18.98	0.73	.24	491	7.42	15.1	2.6	6.2	3.9	16
6-in., deep clay pot*.....	1	25	77	308	14.73	0.59	0.19	421	5.68	13.5	2.6	5.5	3.5	14

* Standard greenhouse pots, sides tapering to base.

† 10 inches deep, sides parallel.

for maximum growth. Nitrate solution was applied to all plants on October 15 and November 27 at the rate of 100 ml. per unit of soil volume (volume of 6-inch clay pot taken as unity). Since the applications had no apparent effect upon the vigor of the plants, nitrogen deficiency which could be so corrected was probably not a limiting factor in any container. The plants were harvested on December 10, 1946, and data were obtained on the oven-dry weights of tops and roots and on root numbers (table 5).

In all containers the emergent stems at final harvest were scattered at random

8-inch glazed pots were well distributed through the soil.

The results in table 5 are an average of the values for the four clones at final harvest. With the exception of the 8-inch glazed container, in which results were similar to those in the 12-inch unglazed clay pot, the columns express the results in order of relative volume of container. The final stem count was positively correlated with soil volume as was the percentage increase in stem number. The dry top weight was much lower in the smaller soil volumes, but the trend was not so regular as with stem numbers.

The top yield per original stem was also somewhat proportional to soil volume, although it was least in the 10-inch shallow clay pot. The weight per final stem did not vary so significantly, though it was highest in the 8-inch glazed pot and lowest in the 10-inch shallow clay pot.

Total root number showed no regular relation to soil volume but was greater in the larger containers and was largest in the 8-inch glazed pot. The second largest total root weight was also produced in the 8-inch glazed pot, which had a relatively low soil volume. Dry root weight in general showed no correlation with soil volume, nor did the weight of each root, but the top-weight/root-weight ratio in general was somewhat proportional to soil volume because of the correlation of top weights with the latter.

The number of roots per stem was fairly constant, regardless of the size of the container. The top yield per root and the weight-per-stem/weight-per-root ratio trended with soil volume.

In summary, in contrast to the relative lack of correlation between root data and soil volume, the tops of the plants showed a direct correlation of total stem numbers and total weight with soil volume (table 5). This positive correlation is also primarily responsible for the direct correlation of soil volume with the top-weight/root-weight ratio, the weight-per-stem/weight-per-root ratio, the top yield per root, and the top yield per original stem.

In all the unglazed clay containers the top growth was in direct proportion to the size of container, but in the glazed crock the top growth far exceeded that attained in a slightly larger unglazed clay pot and was almost equivalent to that attained in a clay pot two and a half times as large. It would thus seem advisable to use glazed pots wherever pos-

sible in preference to unglazed clay, and, if unglazed clay pots must be employed, to use the largest ones possible. The limitation placed upon top growth by the 8-inch clay pots in this experiment would seem to indicate that container size was a limiting factor in both the greenhouse clipping experiment and the shading experiment.

Discussion

Based upon the results of these experiments, certain general recommendations can be made with respect to the culture of *B. inermis* under greenhouse conditions. Since high soil temperatures had very adverse effects upon root growth, especially when photosynthesis was curtailed either by removal of leaf tissue or by shading, it would seem advisable to use large pots and to surround them with sand, peat moss, or some other insulating substance to reduce to a minimum the heating effect upon the soil of the extreme daytime air temperatures reached in summer. The results with containers of different kinds indicated that pot size, shape, and type might be an unforeseen limiting factor in many greenhouse experiments. A deep glazed pot of the largest size that is practicable with available space should be used. When it is necessary to carry greenhouse plants that have been weakened by experimental treatment through natural low light intensities comparable to those in winter in Chicago, the use of supplementary artificial illumination during the normal photoperiod would seem advisable.

However, it should be pointed out that, despite the relatively poor growing conditions in the greenhouse, the effects of two, one, and no clippings upon plants in the greenhouse, as measured by the percentage differences in top weights and stem counts in the three series, were

closely comparable to the effects of similar treatments upon plants in the garden, even though absolute values for these criteria of growth were widely different between greenhouse and garden plants.

Whereas a range of soil temperatures and clipping intensities showed stronger correlation with root growth than with top growth, soil volume exerted its effects most markedly upon the tops.

Summary

1. Vegetative responses of diverse plants of smooth brome grass (*Bromus inermis* Leyss.) to variations in soil temperature, container size, clipping intensity, and shading were investigated in the greenhouses and garden of the University of Chicago with plants derived from both clonal divisions and seed from diverse places of origin. The responses of the individual plants were measured in one or more of the following ways: stem count; total oven-dry top weight; root count; and total oven-dry root weight.

2. The effects of clipping upon plants of diverse origins were studied in three separate experiments: clipping in greenhouse (seventeen clones); clipping in garden (twenty-two clones); and clipping seedlings in greenhouse (three strains of diverse origin). Three series were run in the experiments on clones started in April, 1946: series C, control; series 1, clipped once; and series 2, clipped twice in the 1946 growing season. Throughout the course of the experiments with clonal materials, which were terminated in June, 1947, stem counts were made and dry weights of clipped tops determined. Dry weights of tops and roots were determined for the seedlings. At the final harvest dry weights of tops and roots and the number of stems were inversely proportional to frequency of clipping. In the

greenhouse experiment, where light and temperature as well as container size were limiting factors, the weight per stem did not seem to be affected by clipping, but in the garden experiment it was inversely correlated with frequency of clipping. It was further found that clipping was more adverse in its effects upon root growth than upon top growth and that the effect upon both carried over into the season following clipping.

3. Divisions of four clones were grown at soil temperatures of 20°, 26°, and 31° C. Greatest total top weight was produced at 20° C. in three clones of northern origin and at 26° in one clone of southern origin. At all temperatures the increase in number of stems was less in the clipped series than in the unclipped, and the increase was inversely proportional to the soil temperature. One northern clone did not survive clipping at 31° C., and another died at both the 31° and the 26° soil temperatures. The weight of single roots and the total root weight in each clone showed a much stronger inverse correlation with soil temperature than did total top weight.

4. Three divisions of twenty-three different clones were brought into the greenhouse from the garden and planted in 8-inch clay pots in late April, 1946. One series was placed on a well-lighted bench in the greenhouse, another under a single layer of sheeting, and the third was placed under a double layer of sheeting. Relative light intensities were: outside, 100; greenhouse, 46; one layer of cloth, 14; two layers, 5. At the lowest intensity only four clones survived until the fall of 1946. In the spring of 1947, when the experiment was terminated, ten clones were still alive under the single layer of sheeting, seventeen were still alive in the control series, but none had survived in the most shaded series.

5. Divisions of four clones were grown in unglazed clay pots of five different sizes, in 8-inch glazed pots, and in 12-inch-square wooden boxes. With the exception of the plants in the glazed pots, the final stem count, oven-dry top yield, top yield per original stem, total root number, top-weight/root-weight ratio, top yield per root, and ratio of weight per stem/weight per root were directly proportional to the size of the container. In the glazed pots the plants were as vigor-

ous as in clay pots two and a half times larger.

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DEPARTMENT OF BOTANY AND RANGE ECOLOGY
UNIVERSITY OF ARIZONA
TUCSON, ARIZONA

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